

# Fast $Cl$ -type inhibitory neuron with delayed feedback has non-markov output statistics

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## Abstract

For a class of fast  $Cl$ -type inhibitory spiking neuron models with delayed feedback fed with a Poisson stochastic process of excitatory impulses, it is proven that the stream of output interspike intervals cannot be presented as a Markov process of any order.

**Keywords.** Poisson stochastic process; spiking neuron; probability density function; delayed feedback; fast  $Cl$ -type inhibition; non-Markov stochastic process

## 1 Introduction

Spiking statistics of various neuronal models under a random stimulation has been studied in the framework of two main approaches. The first one is named in [1] as “Gaussian”, because it describes random stimulation by means of Gaussian noise, see e.g. [2]. This approach has developed into the well-known diffusion approximation methodology, see [3]. The second approach is named in [1] as “quantal”, because it takes into account the discrete nature of the influence any input impulse may have on its target neuron. The wide area of research [4, 5, 6] and applications [7, 8, 9] known as spiking neural networks. see [10] for a review, could be considered as utilizing the quantal approach.

For a recent review of mathematically rigorous results as regards neuronal spiking statistics in the both approaches see [11].

We study here mathematically rigorously, in the framework of quantal approach, spiking statistics of inhibitory neuron model belonging to a class of models (see Sec. 2.1, below) with fast  $Cl$ -type inhibitory delayed feedback.

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This construction is stimulated with Poisson stream of excitatory input impulses. For this configuration it was proven in the previous paper [12] for a concrete neuronal model — the binding neuron<sup>1</sup> with threshold 2 —, that statistics of its ISIs is essentially non-Markov. In this paper, we refine and extend methods of [12] making them applicable to any inhibitory neuron with fast *Cl*-type inhibition satisfying a number of simple and natural conditions. Under those conditions, we prove rigorously that ISI statistics of a neuron with delayed fast *Cl*-type inhibitory feedback stimulated with a Poisson stream of input impulses cannot be represented as a Markov chain of any finite order.

A similar statement has been proven recently for a class of excitatory neuronal models [14]. Here we extensively use the approach of paper [14] modifying it as necessary to cover the case of the *Cl*-type fast inhibition.

## 2 Definitions and assumptions

### 2.1 Neuron without feedback

We expect that a neuron satisfies the conditions Cond0-Cond2 of [14]. As regards the Cond3, Cond4 of [14], for the *Cl*-type fast inhibition those conditions should be modified as follows:

- Cond3: Just after firing, neuron appears in its resting state.
- Cond4: The output interspike interval (ISI) distribution can be characterized with a probability density function (pdf)  $p^0(t)$ , which is *continuous* with

$$p^0(0) = 0, \tag{1}$$

positive:

$$t > 0 \Rightarrow p^0(t) > 0, \tag{2}$$

and bounded:

$$\sup_{t>0} p^0(t) < \infty. \tag{3}$$

Also, we impose on the function  $p^0(t)$  the following condition:  $t < 0 \Rightarrow p^0(t) = 0$  in order to have it defined for all real numbers.

The Cond3, above, limits the set of models as compared to [14]. Namely, it claims that the standard state of [14, Cond3] be exactly the resting state of

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<sup>1</sup>Detailed description of the binding neuron model can be found in [13].  
See also [https://en.wikipedia.org/wiki/Binding\\_neuron](https://en.wikipedia.org/wiki/Binding_neuron).

neuron. This requirement is imposed due to the specifics of  $Cl$ -type fast inhibition. Without specifying neuronal model exactly, one can define the resting state as that achieved if the neuron does not receive any input for infinitely long time. For our purpose it is important that after receiving inhibitory impulse, the neuron appears in exactly the same state as immediately after firing. And the state after receiving  $Cl$ -type inhibitory impulse can be only the resting state, see Sec. 2.2.1, below.

The Cond4, above, seems to be as natural for any neuronal model stimulated with Poisson stream as does corresponding condition from [14]. Its difference from [14] has a pure mathematical nature and is suitable for the proof in the case of  $Cl$ -type fast inhibition. It seems, that this conditions are natural for many threshold-type neuronal models known in the literature, see [15, 16, 17, 18] and citations therein. But this still has to be proven by calculating corresponding  $p^0(t)$ . At least, all the five conditions are satisfied for the binding neuron model and for the basic leaky integrate-and-fire (LIF) model, see [19, 20], where  $p^0(t)$  is calculated exactly for each model, respectively.

## 2.2 Feedback line action

We expect that the feedback line satisfies Prop1, Prop2 of [14]. The Prop3 of [14] should be modified for the  $Cl$ -type fast inhibition as follows:

- Prop3: The impulse conveyed to the neuronal input is the fast  $Cl$ -type inhibitory impulse. This means that after receiving such an impulse, the neuron appears in its resting state. This exhausts the action of the inhibitory impulse in a sense that it has no influence on further neuronal states created by next excitatory impulses. It as well does not affect neuron if finds it in its resting state.

### 2.2.1 Biological justification<sup>2</sup>

Neurons, which send inhibitory impulses onto their own body, or dendrites are known in real nervous system, see [21, 22, 23, 24].

The chief inhibitory neurotransmitter in the nervous system is Gamma-aminobutyric acid (GABA). The GABA can activate several types of receptors, the main of which are GABA<sub>a</sub> and GABA<sub>b</sub>. If GABA<sub>a</sub> receptors are activated, the excitable membrane becomes permeable for  $Cl^-$  ions. If a neuron is partially excited, that is its membrane is depolarized to an extent, the  $Cl^-$  current cancels this depolarization since the  $Cl^-$  reversal potential

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<sup>2</sup>see also text in Sec. 2.2 Feedback line action of [14]

is close to the resting potential. For the same reason, the  $Cl^-$  current does not appear if the membrane is at its resting potential. This explains partially where does the Prop3, above, come from. Another case is with GABA<sub>b</sub> receptors activation. This causes  $K^+$  ions permeability. The outward  $K^+$  current is able to hyperpolarize membrane even below its resting potential. The remarkable difference between GABA<sub>a</sub> and GABA<sub>b</sub> mediated inhibition is rather different kinetics of the corresponding  $Cl^-$  and  $K^+$  currents. Namely, according to [25], the  $Cl^-$  current rise time is 1 - 5 ms, and the decay time constant is about 10 - 25 ms. The  $K^+$  current rise time is 10 - 120 ms, and the decay time constant is about 200 - 1600 ms. The  $K^+$  current can be even slower, see [23, 26, 27]. Having in mind this contrast in the speed of  $Cl^-$  and  $K^+$  transients, we idealize the  $Cl^-$  current kinetics as having infinitesimally short rise time and infinitely fast decay, both can be achieved with infinitely large  $Cl^-$  conductance at the moment of receiving inhibitory impulse. This additionally explains where does the Prop3, above, come from.

Finally, it should be mentioned that our consideration will be valid also for artificial hardware neurons, see [28, 29], and abstract neurons used in mathematical studies, provided Cond0-Cond4 and Prop1-Prop3, above, are satisfied.

The important for us consequence of Prop2 of [14] is that at any moment of time the feedback line is either empty, or conveys a single impulse. If it does convey an impulse, then its state can be described with a stochastic variable  $s$ ,  $s \in ]0; \Delta]$ , which we call further “time to live”. The variable  $s$  denotes the exact time required by the impulse to reach the output end of the line, which is the neuron’s input for inhibitory impulses, and to leave the line. Here,  $\Delta$  denotes the delay duration in the feedback line.

### 3 Results

Our purpose here is to prove the following Theorem<sup>3</sup>:

**Theorem 1** *Let a neuronal model satisfies conditions Cond0-Cond4, above. Expect that the model is extended by introducing a delayed **fast Cl-type inhibitory** feedback line, which satisfies the Prop1-Prop3, above. Then, in the stationary regime, the output stream of ISIs of the neuron cannot be presented as a Markov chain of any finite order.*

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<sup>3</sup>A similar theorem for the **excitatory** feedback line has been proven in [14]

### 3.1 Proof outline<sup>4</sup>

Let  $p^{inh}(t_{n+1} | t_n, \dots, t_0)dt_{n+1}$  denotes the conditional probability to get the duration of  $(n+2)$ -nd ISI in the interval  $[t_{n+1}; t_{n+1} + dt_{n+1}[$  provided that previous  $n+1$  ISIs had duration  $t_n, \dots, t_0$ , respectively. From the definition in [30, Ch.2 §6], one can obtain the necessary condition

$$p^{inh}(t_{n+1} | t_n, \dots, t_1, t_0) = p^{inh}(t_{n+1} | t_n, \dots, t_1), \quad t_i \in \mathbb{R}^+, i = 0, \dots, n+1, \quad (4)$$

required for the stochastic process  $\{t_j\}$  to be  $n$ th order Markov chain.

We intend to prove that the relation (4) does not hold for any  $n$ . For this purpose we calculate exact expression for  $p^{inh}(t_{n+1} | t_n, \dots, t_0)$  as

$$p^{inh}(t_{n+1} | t_n, \dots, t_0) = \frac{p^{inh}(t_{n+1}, t_n, \dots, t_0)}{p^{inh}(t_n, \dots, t_0)} \quad (5)$$

from which it will be clearly seen that the  $t_0$ -dependence in  $p^{inh}(t_{n+1} | t_n, \dots, t_0)$  cannot be eliminated whatever large the  $n$  is. In the Eq. (5), expression  $p^{inh}(t_n, \dots, t_1)$  denotes the joint probability density function of ISIs duration of neuron with the fast  $Cl$ -type inhibitory delayed feedback.

Let us introduce the conditional joint probability density  $p^{inh}(t_{n+1}, \dots, t_0 | s)$ , which denotes the conditional probability density to get  $n+2$  consecutive ISIs  $\{t_{n+1}, \dots, t_0\}$  provided that at the beginning of the first ISI ( $t_0$ ) the time to live of impulse in the feedback line was equal to  $s$ . This conditional probability can be used to calculate required joint pdfs as follows

$$p^{inh}(t_{n+1}, \dots, t_0) = \int_0^\Delta p^{inh}(t_{n+1}, \dots, t_0 | s) f^{inh}(s) ds, \quad (6)$$

where  $f^{inh}(s)$  is the stationary pdf which describes distribution of times to live at the beginning of any ISI in the stationary regime.

In what follows we analyze the structure of functions  $f^{inh}(s)$  and  $p^{inh}(t_{n+1}, \dots, t_0 | s)$ . It appears that  $f^{inh}(s)$  has a singular component  $a\delta(s - \Delta)$  with  $a > 0$ , and  $p^{inh}(t_{n+1}, \dots, t_0 | s)$  has jump discontinuities at definite hyperplanes in the  $(n+3)$ -dimensional space of its variables  $(t_{n+1}, \dots, t_0, s)$ . After integration in (6), some of those discontinuities will survive in the  $(n+2)$ -dimensional space of variables  $(t_{n+1}, \dots, t_0)$ , and one of those survived has its position depending on  $t_0$ . The  $t_0$ -dependent jump discontinuity will as

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<sup>4</sup>The proof outline is very similar to that of [14], therefore, it is abridged here. Please, consult with [14].

well survive in the  $p^{inh}(t_{n+1} | t_n, \dots, t_0)$  for any  $n$ , provided that  $t_n, \dots, t_0$  satisfy the following condition:

$$\sum_{i=0}^n t_i < \Delta, \quad (7)$$

where  $\Delta > 0$  is the full delay time in the feedback line. Taking into account that the equation in the necessary condition (4) must hold for any set of  $t_{n+1}, \dots, t_0$ , we conclude that (4) cannot be satisfied for any  $n$ .

## 3.2 The proof

### 3.2.1 Structure of functions $p^{inh}(t_{n+1}, \dots, t_0 | s)$

Specifics of the feedback line action together with condition (7) results in a very simple structure of  $p^{inh}(t_{n+1}, \dots, t_0 | s)$  at different parts of the integration domain in (6). Those parts are defined as follows:

$$D_k = \{s | \sum_{i=0}^{k-1} t_i < s \leq \sum_{i=0}^k t_i\}, \quad k = 0, \dots, n,$$

$$D_{n+1} = \{s | \sum_{i=0}^n t_i < s \leq \Delta\}.$$

As regards the structure itself, the following representation can be derived similarly as it was done in [14]:

$$\begin{aligned} p^{inh}(t_{n+1}, \dots, t_0 | s) &= \\ &= p^{inh}(t_{n+1}, \dots, t_{k+1} | \Delta) p^{inh}\left(t_k | s - \sum_{i=0}^{k-1} t_i\right) \prod_{i=0}^{k-1} p^0(t_i), \\ &\quad s \in D_k, \quad k = 0, \dots, n, \end{aligned} \quad (8)$$

$$p^{inh}(t_{n+1}, \dots, t_0 | s) = p^{inh}\left(t_{n+1} | s - \sum_{i=0}^n t_i\right) \prod_{i=0}^n p^0(t_i), \quad s \in D_{n+1}. \quad (9)$$

$$p^{inh}(t_{n+1}, \dots, t_{k+1} | \Delta) = p^{inh}\left(t_{n+1} | \Delta - \sum_{i=k+1}^n t_i\right) \prod_{i=k+1}^n p^0(t_i). \quad (10)$$

Here  $p^{inh}(t | s)$  denotes the conditional pdf to get ISI of duration  $t$  if at its beginning, time to live of impulse in the feedback line is  $s$ .

Representation of  $p^{inh}(t_{n+1}, \dots, t_0 | s)$  by means of  $p^0(t)$  and  $p^{inh}(t | s)$  found here is similar to that found in [14] for the excitatory case. But the structure of function  $p^{inh}(t | s)$ , used in that representation, is different.

### 3.2.2 Structure of function $p^{inh}(t | s)$

Expect that at the beginning of an ISI, there is an impulse in the feedback line with time to live  $s$ . Then the probability that this ISI will have its duration  $t < s$  does not depend on the feedback line presence. Therefore,

$$t < s \Rightarrow p^{inh}(t | s) = p^0(t). \quad (11)$$

In the opposite situation, receiving of an ISI duration greater than  $s$  happens if (i) the neuron does not fire during interval  $]0; s[$  and (ii) the neuron starts at its resting state (Prop3, above) at the moment  $s$  and fires at  $t > s$ . Realizations of events (i) and (ii) depend on disjoint segments of the input Poisson stream. Therefore, (i) and (ii) are statistically independent. The probability of (i) is as follows:

$$\mathbf{P}^0(s) = 1 - \int_0^s p^0(t) dt. \quad (12)$$

The probability of (ii) is  $p^0(t - s)$ . This gives

$$t > s \Rightarrow p^{inh}(t | s) = \mathbf{P}^0(s)p^0(t - s). \quad (13)$$

It can be concluded from (11) and (13) that

$$\lim_{t \uparrow s} p(t | s) = p^0(s) \quad \text{and} \quad \lim_{t \downarrow s} p(t | s) = 0.$$

Now, taking into account (1) and (2) from Cond4, above, we conclude that the function  $p^{inh}(t | s)$  considered as a function of two variables  $(t, s)$ ,  $t \geq 0$ ,  $s \in ]0; \Delta]$  has a jump discontinuity along the straight line  $t = s$ . The magnitude of this jump is  $p^0(s)$ , and it is strictly positive for positive  $t$ . Concrete values of  $p^{inh}(t | s)$  along the line  $t = s$  does not matter and can be chosen arbitrarily.

Finally, for  $p^{inh}(t | s)$  we have<sup>5</sup>

$$p^{inh}(t | s) = \chi(s - t)p^0(t) + \mathbf{P}^0(s)p^0(t - s), \quad (14)$$

where  $\chi(s)$  is the Heaviside step function.

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<sup>5</sup>Compare this with [31, Eq. (11)], where  $p^{inh}(t | s)$  is calculated exactly for the binding neuron model.

### 3.2.3 Structure of probability density function $f^{inh}(s)$

It appeared that the structure of  $f^{inh}(s)$  is exactly the same as it was found in [14] for the excitatory case. This structure is as follows<sup>6,7</sup>

$$f^{inh}(s) = g(s) + a\delta(s - \Delta), \quad (15)$$

where  $a > 0$  and  $g(s)$  is bounded continuous function vanishing out of interval  $]0; \Delta[$ .

### 3.2.4 Form of $p^{inh}(t_{n+1}, \dots, t_0)$ and $p^{inh}(t_n, \dots, t_0)$ after integration in (6)

Let  $D = \bigcup_{k=0}^n D_k$ . At  $D$ , representations (8) and (10) are valid. Also at  $D$ ,  $f^{inh}(s)$  reduces to  $g(s)$ . Therefore,

$$\begin{aligned} \int_D p^{inh}(t_{n+1}, \dots, t_0 | s) f^{inh}(s) ds = \\ = \sum_{k=0}^n p^{inh} \left( t_{n+1} | \Delta - \sum_{i=k+1}^n t_i \right) \times \\ \times \prod_{\substack{i=0 \\ i \neq k}}^n p^0(t_i) \int_{D_k} p^{inh} \left( t_k | s - \sum_{j=0}^{k-1} t_j \right) g(s) ds. \end{aligned} \quad (16)$$

The first factor (with fixed  $k$ ,  $0 \leq k \leq n$ ) in the r.h.s. of Eq. (16) is as follows:

$$p^{inh} \left( t_{n+1} | \Delta - \sum_{i=k+1}^n t_i \right).$$

Due to Eq. (14), this factor does have a jump discontinuity along the hyperplane  $\sum_{i=k+1}^{n+1} t_i = \Delta$  in the space of variables  $(t_0, \dots, t_{n+1})$ . Notice, that the position of this hyperplane does not depend on  $t_0$  for any  $k \in \{0, \dots, n\}$ .

The second factor in the r.h.s. of Eq. (16) is as follows:  $\prod_{\substack{i=0 \\ i \neq k}}^n p^0(t_i)$ , and

it is continuous.

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<sup>6</sup>The proof can be found in [14].

<sup>7</sup>Compare this with [32, Eqs. (14)-(16)], where  $f(s)$  is calculated exactly for the binding neuron model.



The third factor in the r.h.s. of Eq. (16) can be transformed as follows:

$$\begin{aligned}
\int_{D_k} p^{inh} \left( t_k \mid s - \sum_{j=0}^{k-1} t_j \right) g(s) ds &= \int_{\sum_{j=0}^{k-1} t_j}^{\sum_{j=0}^k t_j} p^{inh} \left( t_k \mid s - \sum_{j=0}^{k-1} t_j \right) g(s) ds = \\
&= \int_0^{t_k} p^{inh}(t_k \mid s) g \left( s + \sum_{j=0}^{k-1} t_j \right) ds = \int_0^{t_k} \mathbf{P}^0(s) p^0(t_k - s) g \left( s + \sum_{j=0}^{k-1} t_j \right) ds.
\end{aligned} \tag{17}$$

The last expression is continuous with respect to variables  $(t_0, \dots, t_{n+1})$ . Therefore, one can conclude that expression (16) does not have a jump discontinuity, which position depends on  $t_0$ .

Consider now the remaining part of integral in (6). With (9) taken into account one has:

$$\begin{aligned}
\int_{D_{n+1}} p^{inh}(t_{n+1}, \dots, t_0 \mid s) f^{inh}(s) ds &= \\
&= \prod_{i=0}^n p^0(t_i) \int_{D_{n+1}} p^{inh} \left( t_{n+1} \mid s - \sum_{i=0}^n t_i \right) f^{inh}(s) ds.
\end{aligned} \tag{18}$$

Here, the first factor,  $\prod_{i=0}^n p^0(t_i)$  is continuous and strictly positive for positive  $t_i$ . The second factor can be transformed as follows:

$$\begin{aligned}
\int_{D_{n+1}} p^{inh} \left( t_{n+1} \mid s - \sum_{i=0}^n t_i \right) f^{inh}(s) ds &= \\
&= \int_{\sum_{i=0}^n t_i}^{\Delta} p^{inh} \left( t_{n+1} \mid s - \sum_{i=0}^n t_i \right) f^{inh}(s) ds = \\
&= \int_0^{\Delta - \sum_{i=0}^n t_i} p^{inh}(t_{n+1} \mid s) f^{inh} \left( s + \sum_{i=0}^n t_i \right) ds.
\end{aligned} \tag{19}$$

Now, let us use representations (14) and (15) in order to figure out which kind of discontinuities does the expression (19) have. Due to (14) and (15), expression (19) will have four terms. The first one we get by choosing the first term both in (14) and (15):

$$A_{11} = \int_0^{\Delta - \sum_{i=0}^n t_i} \chi(s - t_{n+1}) p^0(t_{n+1}) g\left(s + \sum_{i=0}^n t_i\right) ds.$$

This term is either equal to zero, if  $t_{n+1} > \Delta - \sum_{i=0}^n t_i$ , or otherwise transforms into a continuous function of variables  $(t_0, \dots, t_{n+1})$ . Moreover,

$$\lim_{t_{n+1} \uparrow \Delta - \sum_{i=0}^n t_i} A_{11}(t_{n+1}) = 0.$$

The second one we get by choosing the second term in (14) and the first term in (15):

$$A_{21} = \int_0^{\Delta - \sum_{i=0}^n t_i} \mathbf{P}^0(s) p^0(t_{n+1} - s) g\left(s + \sum_{i=0}^n t_i\right) ds.$$

This is as well a continuous function of variables  $(t_0, \dots, t_{n+1})$ .

The third one we get by choosing the first term in (14) and the second term in (15):

$$\begin{aligned} A_{12} &= a \int_0^{\Delta - \sum_{i=0}^n t_i} \chi(s - t_{n+1}) p^0(t_{n+1}) \delta\left(\sum_{i=0}^n t_i + s - \Delta\right) ds = \\ &= a \chi\left(\Delta - \sum_{i=0}^{n+1} t_i\right) p^0(t_{n+1}). \end{aligned} \quad (20)$$

This term has a jump discontinuity along the hyperplane

$$\sum_{i=0}^{n+1} t_i = \Delta. \quad (21)$$

The forth one we get by choosing the second term in (14) and the second term in (15):

$$\begin{aligned} A_{22} &= a \int_0^{\Delta - \sum_{i=0}^n t_i} \mathbf{P}^0(s) p^0(t_{n+1} - s) \delta \left( \sum_{i=0}^n t_i + s - \Delta \right) ds = \\ &= \mathbf{P}^0 \left( \Delta - \sum_{i=0}^n t_i \right) p^0 \left( \sum_{i=0}^{n+1} t_i - \Delta \right). \end{aligned}$$

This is as well a continuous function of variables  $(t_0, \dots, t_{n+1})$ .

After taking into account the above reasoning, we conclude that the required joint probability density has the following form

$$p^{inh}(t_{n+1}, \dots, t_0) = p^w(t_{n+1}, \dots, t_0) + a\chi \left( \Delta - \sum_{i=0}^{n+1} t_i \right) \prod_{j=0}^{n+1} p^0(t_j). \quad (22)$$

where function  $p^w(t_{n+1}, \dots, t_0)$  does not have a jump discontinuity depending on  $t_0$ , and the second term in (22) does have such a discontinuity along the hyperplane (21).

*Form of  $p^{inh}(t_n, \dots, t_0)$  after integration*

If (7) is satisfied, then we have similarly to (8), (9)

$$\begin{aligned} p^{inh}(t_n, \dots, t_0 | s) &= \\ &= p^{inh}(t_n, \dots, t_{k+1} | \Delta) p^{inh} \left( t_k | s - \sum_{i=0}^{k-1} t_i \right) \prod_{i=0}^{k-1} p^0(t_i), \\ &\quad s \in D_k, \quad k = 0, \dots, n-1, \\ p^{inh}(t_n, \dots, t_0 | s) &= p^{inh} \left( t_n | s - \sum_{i=0}^{n-1} t_i \right) \prod_{i=0}^{n-1} p^0(t_i), \quad s \in D_n. \end{aligned}$$

Again due to (7), and in analogy with (10) we have instead of the last two equations the following one:

$$\begin{aligned} p^{inh}(t_n, \dots, t_0 | s) &= p^{inh} \left( t_k | s - \sum_{i=0}^{k-1} t_i \right) \prod_{\substack{i=0 \\ i \neq k}}^n p^0(t_i), \\ &\quad s \in D_k, \quad k = 0, \dots, n. \quad (23) \end{aligned}$$

It is clear that expression similar to (9) turns here into the following

$$p^{inh}(t_n, \dots, t_0 | s) = \prod_{i=0}^n p^0(t_i), \quad s \in D_{n+1}. \quad (24)$$

Now, due to (23), (24) we have

$$\begin{aligned} p^{inh}(t_n, \dots, t_0) &= \int_0^\Delta p^{inh}(t_n, \dots, t_0 | s) f^{inh}(s) ds = \\ &= \sum_{k=0}^n \prod_{\substack{i=0 \\ i \neq k}}^n p^0(t_i) \int_{D_k} p^{inh} \left( t_k | s - \sum_{i=0}^{k-1} t_i \right) g(s) ds + \prod_{i=0}^n p^0(t_i) \int_{D_{n+1}} f^{inh}(s) ds. \end{aligned} \quad (25)$$

From calculations similar to those made in Eq. (17) it can be concluded that  $p^{inh}(t_n, \dots, t_0)$  is continuous at the domain defined by (7).

### 3.2.5 $t_0$ -dependence cannot be eliminated in $p^{inh}(t_{n+1} | t_n, \dots, t_0)$

Now, with representations (22) for  $p^{inh}(t_{n+1}, \dots, t_0)$  and (25) for  $p^{inh}(t_n, \dots, t_0)$  we can pose a question about the form of  $p^{inh}(t_{n+1} | t_n, \dots, t_0)$ . The latter can be found as defined in (5). First of all notice that due to (25) and Cond4,  $p^{inh}(t_n, \dots, t_0)$  is strictly positive for positive ISIs. This allows us to use it as denominator in the definition (5). Second, it can be further concluded from (25) and Cond4, that  $p^{inh}(t_n, \dots, t_0)$  is bounded. The latter together with continuity of  $p^{inh}(t_n, \dots, t_0)$  means that any discontinuity of jump type present in the  $p^{inh}(t_{n+1}, \dots, t_0)$  appears as well in the  $p^{inh}(t_{n+1} | t_n, \dots, t_0)$ . It follows from the above and from Eq. (22) that the conditional pdf  $p^{inh}(t_{n+1} | t_n, \dots, t_0)$  can be represented in the following form:

$$\begin{aligned} p^{inh}(t_{n+1} | t_n, \dots, t_0) &= p^w(t_{n+1} | t_n, \dots, t_0) + \\ &+ Z(t_{n+1}, \dots, t_0) \chi \left( \Delta - \sum_{i=0}^{n+1} t_i \right), \end{aligned} \quad (26)$$

where  $p^w(t_{n+1} | t_n, \dots, t_0)$  does not have any jump type discontinuity which position depends on  $t_0$ , and  $Z(t_{n+1}, \dots, t_0)$  is strictly positive function:

$$Z(t_{n+1}, \dots, t_0) = \frac{a \prod_{i=0}^{n+1} p^0(t_i)}{p(t_n, \dots, t_0)}.$$

The representation (26) thus proves that for any  $n$ , conditional pdf  $p^{inh}(t_{n+1} | t_n, \dots, t_0)$  does depend on  $t_0$  (the second term in (26)) and this dependence cannot be eliminated.  $\square$

## 4 Conclusions and Discussion

Conclusions made in [14] for the class of **excitatory** neuronal models are as well valid for the studied here case of the class of **fast Cl-type inhibitory** neuronal models. Therefore, we do not replicate the text here in order to minimize overlap with the previous paper.

At the same time, it is worth mentioning that the question of to how extent the Poisson hypothesis is acceptable in neuroscience has been already discussed, see [33]. The experimentally observed presence of memory in the ISIs output of real neurons has been reported many times, see [34, 35, 36, 37, 38]. Also several theoretical models of how the memory could appear are offered, see [16, 39, 40, 41, 42, 43].

One more basic reason for non-Markov statistics in a neuronal network is revealed by B. Cessac in [44], where the discrete time model network of the standard leaky integrate-and-fire neurons is considered. In this model, the interneuronal communication lines have zero delays and external input is deterministic, but synaptic weights are subjected to uncorrelated random fluctuations. For this model, it is established in [44] that the stochastic process, which output is the set of firing states of all neurons the network is composed of, will be non-Markovian as well. What could be the reason of memory appearance in the stochastic process of neuronal firing states if there are no delays in this model? The effect may be explained as follows. Any LIF neuron in the network considered loses memory about its previous states at firing moment. But neurons, which do not fire at that same moment, still retain their memory about their previous states. Therefore, the whole network retains some information about its previous state after firing of any individual neuron (provided all neurons do not fire synchronously) the network is composed of. The instantaneous firing state of the network specifies which neurons are in the firing state at a given moment  $t$ , but says nothing about state of neurons, which are quiescent at that moment. Knowledge of earlier firing states of the network can improve our predicting ability as regards states of the quiescent neurons at the moment  $t$ , and finally, as regards the network firing state at the next moment,  $t + 1$ . This brings about a memory into the network's stochastic activity. On the other hand, individual neurons in such a network can still have a Poisson-like activity, if not considered together, see example in [45].

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